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Den förlängda fenotypen i granens krontak

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Department of Wildlife, Fish, and Environmental studies

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Abstract

The extended phenotype may help us understand how genetically determined trait variation in foundation species can influence associated organisms. Today, there is no existing demonstration of how genetically determined trait variation in Norway spruce (*Picea abies*) may affect associated organisms in tree canopies. As a majority of all planted Norway spruce seedlings used, in Swedish forestry today, originates from breeding programs it is interesting to know how the genetic material used in these programs may affect associated organisms. For example, according to the growth rate hypothesis the nutritional status of a plant should correspond negatively with tree growth, and the nutritional status of the plant should affect associated organisms. In this study, I aim to evaluate if the genetic origin of Norway spruce affect plant growth and nutritional status of needles (in this case the C:N ratio) and in extension associated communities (abundance of aphids) in the tree canopies. More specifically I will test the following six hypotheses; (1) there is a genetic influence on growth so that breast height diameter (DBH) differ among full-sib families, (2) the growth rate of the trees expressed as their DBH have a significant negative effect on needle C and positive effect on N and consequently negative effect on the C:N ratio, (3) there is a genetic component influencing C:N ratio of the needles so that the ratio differs between full-sib families, (4) growth rate of different full-sib families effect the C:N ratio of needles, (5) the abundance of aphids is influenced by full-sib family and the C:N ratio of needles and (6) growth rate of different full-sib families effect the abundance of aphids. To address these hypotheses twig and insect samples was sampled from Norway spruce trees in 90 two-by-two tree plots from 9 full-sib families. Aphids were determined to species level and needles was analyzed for C and N content with an elemental analyzer. The data on tree growth, needle chemistry, and aphid abundance were used in statistical tests using the statistical software JMP PRO 12.1.0.

I found a clear genetic influence on growth in Norway spruce; fast growing full-sib families reached a DBH almost three times larger than that of slow growing full-sib families after 37 years (3.8 cm vs. 9.8 cm). In line with the growth rate hypothesis differences in growth rate also corresponded negatively with the C:N ratio of needles suggesting that needles of fast growing trees are more nutritious than slow growing trees. Despite this relation fast growing full-sib families did not necessarily have the highest nutritional status suggesting that the growth rate – nutrition relationship follow different developmental trajectories in different families. Further, aphid abundance in the canopy of Norway spruce was significantly influenced by full-sib family, but this effect could not be related to tree growth nor C:N ratio of the needles of the different full-sub families.

Given these results, it seems possible that selection of plant material of certain genetic origin (e.g. fast growing plants) such as currently conducted in Sweden can influence how other plant traits are expressed in populations. If these other traits are of ecological significance we would also expect them to influence ecological processes.

Introduction

The extended phenotype, defined by Dawkins (1982) as “all effects of a gene upon the world” and later by Whitham *et al.* (2003) as “the effects of genes at levels higher than the population”, may help us understand how genetically determined trait variation in foundation species influence associated organisms (Whitham *et al.*, 2003; Dickson & Whitham, 1996). This effect can be pronounced and is shown in a number of studies from various study systems (Whitham *et al.*, 2012; Whitham *et al.*, 2006; Iason *et al.*, 2005; Ito & Ozaki, 2005; Dungey *et al.*, 2000; Hwang & Lindroth, 1997; Maddox & Root, 1990). Nevertheless, there is still little known about the effects of genetically determined trait variation in boreal trees on associated organisms (Whitham *et al.*, 2006), but see Korkama *et al.* (2008, 2007, & 2006) for examples in soil.

In Norway spruce phenotypic variation are shown in various ecological important traits such as the number of branches (Steffenrem *et al.*, 2008), dehardening (Westin *et al.*, 2000), and Rosner *et al.* (2007) showed that mechanical toughness and growth rate are positively related. There is also a genotypic correlation with fungal growth in Norway spruce (Swedjemark *et al.*, 1997) and Axelsson *et al.* (2015) showed that carbon based defence (phenolics) in Norway spruce differed significantly among full-sib families. The above studies clearly show that the phenotypic variation in Norway spruce can be significant, but the effect of such variation on associated organisms are not well-known. Further, such studies have merely touched upon how commercially important traits such as growth may affect ecologically important traits and further the extended phenotypes associated with the tree.

General theory on plant physiology predicts that plant growth will affect the nutritional status of the plant (e.g. C:N ratio) by a synchronous effect on nutrition (N) and carbon based ‘defensive’ characteristics. The growth rate hypothesis states that there is a correlation between the stochasticity of C:N:P and the growth of an organism (Elser *et al.*, 2000). Peng *et al.* (2011) found a positive relation between N concentrations and growth. Also, trade-offs between growth and defence suggests that plants with fast growth should be less defended, as phenolic and alkaloid synthesis directly competes with growth (Herms & Mattson, 1992). Addressing how these synchronic effects on growth play out to affect plant nutrition (C:N ratio) could help in our understanding of how plant growth may affect associated organisms.

The nutritional status of foliage is an ecologically important trait of general influence over various herbivores. A high C:N ratio translates to a low concentration of N, and consequently, less protein for the herbivore (Mattson, 1980). Kainulainen *et al.* (1996) reported an increase in aphid growth when foliar nitrogen increased due to fertilization. Similar results are shown by Fajer (1989) that found that N content in *Plantago lanceolata* leaves correlated positively with growth of larvae of the butterfly *Junonia coenia*. In a study by Williams and Avakian (2015) a genetic effect on foliar terpenes was shown and the variation among clones in the colonization by aphids could be explained by terpenes. Consequently, if a plant growth affect plant nutrition we would expect that this would influence other organisms associated with the plant.

Links between commercially important traits such as growth and other ecologically important properties are not well studied in Norway spruce, and basically nothing is known about how genetics can affect extended phenotypes in tree canopies. In this study, I will examine the effect

of spruce genetics and genetically determined growth on the nutritional status of trees and further on the abundance of aphids of the genus *Cinara* utilizing spruce foliage. More specifically, I will test the following hypotheses.

- 1: There is a genetic influence on growth so that breast height diameter (DBH) differ among full-sib families.
- 2: The growth rate of the trees expressed as their DBH have a significant negative effect on needle C and positive effect on N and consequently negative effect on the C:N ratio.
- 3: There is a genetic component influencing C:N ratio of the needles so that the ratio differs between full-sib families.
- 4: Growth rate of different full-sib families effect the C:N ratio of needles.
- 5: The abundance of aphids is influenced by full-sib family and the C:N ratio of needles.
- 6: Growth rate of different full-sib families effect the abundance of aphids.

Material and methods

Experimental design

The field work for this study was conducted in Sävar (63°88'N 23°55'E, altitude 10m) about 15 km northeast of Umeå on a test site (ID No S23F7720331) managed by The Forest Research Institute of Sweden (Skogforsk). The experiment was established in 1977. Norway spruce (*Picea abies*) seedlings were planted with 1x1m gaps from each other in a design so that four trees in a two-by-two tree plots were from the same full-sib family (fig 1). The different full-sib families originated from controlled crosses between mothers and fathers from different locations throughout the counties of Västerbotten, Jämtland and Västernorrland. These two-by-two plots are considered a sampling unit (replicate) in these studies.

Sampling and aphid species determination

In the autumn of 2014 (16/9 – 27/10) spruce trees from 90 two-by-two tree plots from nine full-sibs differing in growth rate were surveyed. However, due to mortality nine plots could not be sampled and the data presented here is from 81 plots. From the lowest green branch of each tree one green twig was collected. The size of twigs was standardized to fit in a 25x20 cm zip-bag. The twigs were stored frozen and later processed in the lab. Each frozen twig was pulled through the hand five times to detach aphids on to a tray. Aphids were collected and stored in ethanol for later species determination.

All aphid species were determined to species level using the entomological identification manual Fauna Entomologica Scandinavica (Heie, 1980) and (Heie, 1995). Aphids were put on a petri dish with ethanol and examined under a microscope (Leica, Upplands Väsby, Sweden) down to 4X magnification.

Chemicals analyses

For chemical analyses (C, N) needles were collected from the most peripheral of the current year's shoot of each twig in September 2015. Each needle sample consisted of 24 needles collected in equal numbers from the live trees in each plot. The needles from all 81 samples were put in separate paper bags and put into a drying cabinet for 48 hours on 50° (C) before milled in a sample mill (1093 Cyclotec sample mill, FOSS, Hillerød, Denmark) for approximately 10 seconds. The milled samples were put in Eppendorf test tubes.

Measurement of mass fractions of C and N (ω_C and ω_N) was done using an elemental analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). C and N of the dried sample

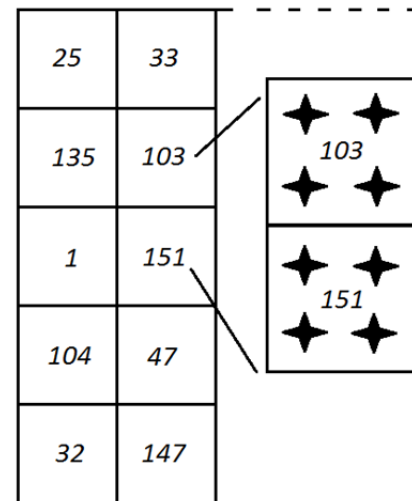


Figure 1. Principal sketch of the experimental design. Numbers are family id and stars show the placement of four individual trees used as a replicate. Each family was replicated 9-10 times.

material are converted to CO₂ and N₂ by combustion, dry mass is defined by oven drying at 70° (C) for minimum 18 hours. The results are corrected for drift and sample size effect (non-linearity). Working standards are wheat and maize flours calibrated against reference standards. For ω N, atropine, cellulose, and NIST 1515 apple leaves, and for ω C, cyclohexanone, nicotinamide, and sucrose.

Statistical analyses

To test my hypotheses I used a combination of statistical tests (Table 1). I used linear regressions to fit DBH against needle chemistry and further needle chemistry against aphid abundance to test the relationship between my continuous independent variables and the responses. To test the effect on full-sib family on DBH, needle chemistry and aphid abundance I used a Generalized Linear Model (GLM). In this test, I also included DBH as a covariate for the test on needle chemistry and needle chemistry as a covariate for aphid abundance. As the distribution of the aphid data was skewed to the left with many zeros the GLM on aphid abundance was fitted with Poisson distribution. In this case, the non-parametric Kruskal-Wallis test was used as a post hoc test to explore significant differences in means. The data were otherwise normal distributed and Tukey-Kramer HSD test was used to find means that were significant different from each other. All the analyses described above were done using the statistical program JMP PRO 12.1.0 (© 2015 SAS Institute Inc.).

Table 1. *Data distribution and test for each hypothesis*

Hypothesis	Data distribution	Data response	Test
1	Normal	DBH	GLM & Tukey-Kramer
2	Normal	N, C and C:N ratio	Linear regression
3	Normal	C:N, DBH as control	GLM & Tukey-Kramer
4	Normal	C:N	Linear regression
5	Poisson	Aphid abundance	GLM & Kruskal-Wallis
6	Poisson	Aphid abundance	Linear regression

Result

1: There is a genetics influence on growth so that DBH differ among full-sibs families.

The GLM on the effect of full-sib family on DBH show that there is a clear genetic influence on growth in Norway spruce ($P = 0.0001$, $df = 8$, $\text{Chi}^2 = 32.3$). In some cases this effect caused fast growing full-sib families to have a DBH that were twice as high compared with slow growing families (Fig 2). Comparison for all pairs using Tukey-Kramer HSD also shows that full-sib 126 grew significantly faster than full-sib 45, 138, 8, 70, and 71.

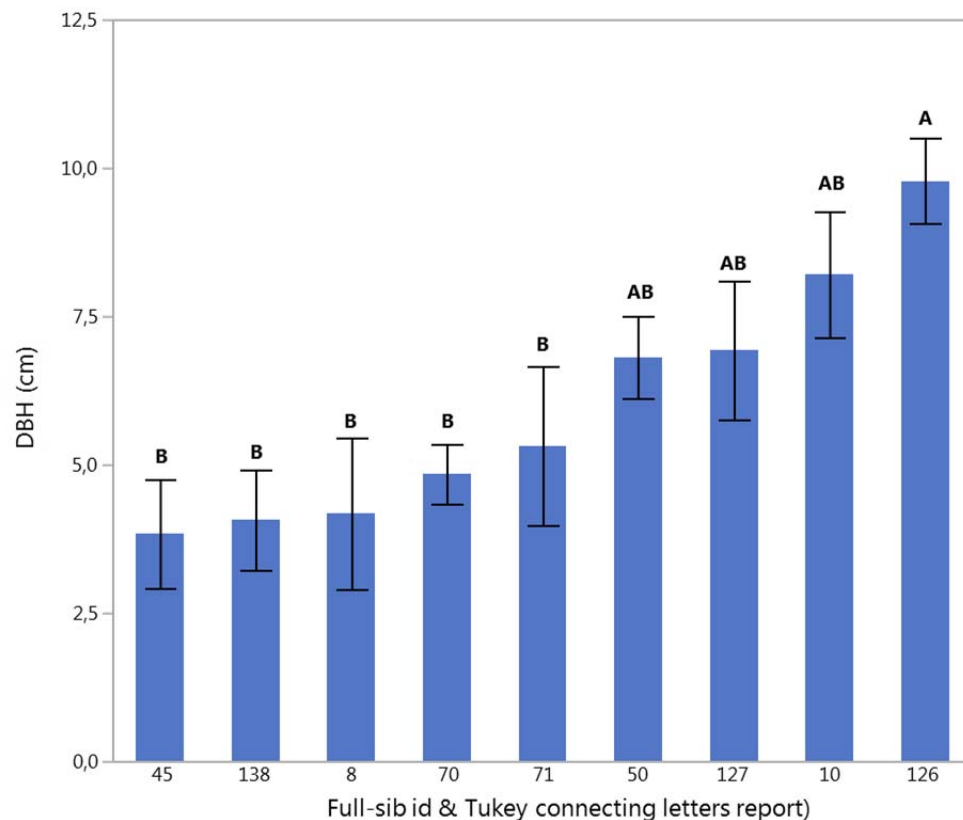


Figure 2. Bar graph showing the mean DBH (as a proxy of growth rate) of 9 different full-sibs families of Norway spruce trees. Error bars showing standard error. A & B symbolizes the all pair comparison using Tukey method, showing that 126 differs significantly from 45, 138, 8, 70, and 71.

2: The growth rate of the trees expressed as their DBH have a significant negative effect on needle C and positive effect on N and consequently negative effect on the C:N ratio.

DBH clearly had a positive effect ($P = 0.0008$, $R^2 = 0.1167$) on N content in the needles and consequently a negative effect on the C:N ratio ($P = 0.0008$, $R^2 = 0.1167$). There was no significant relationship between DBH and C content ($P = 0.7142$, $R^2 = 0.0015$).

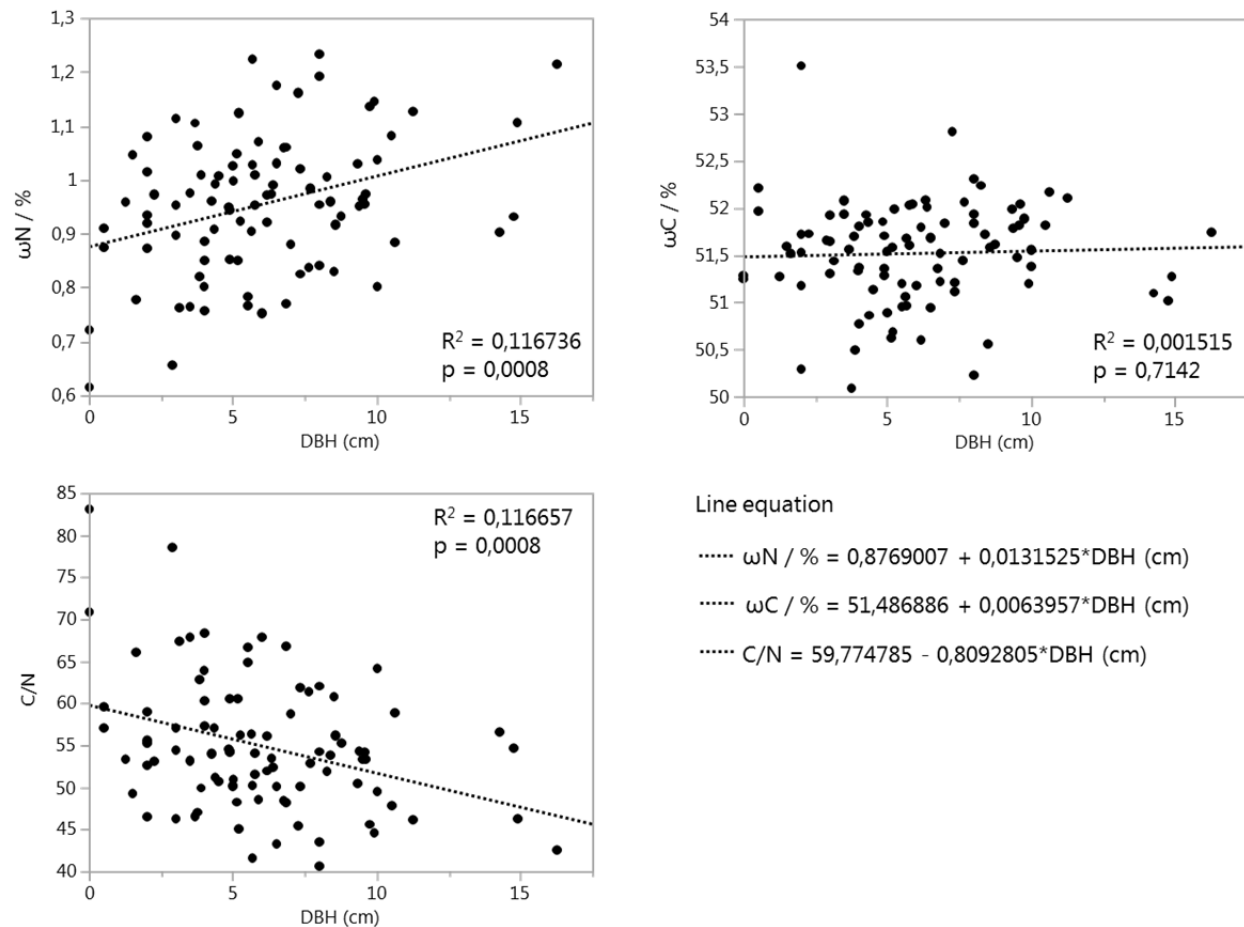


Figure 3 Linear regressions on needle chemistry e.g. percentage of C and N, and the C:N ratio and DBH with corresponding line equation, R^2 value, and P -value.

3: There is a genetic component influencing C:N ratio of the needles so that the ratio differs between full-sib families.

The C:N ratio differed significantly between full-sib families ($P = 0.0205$, $df = 8$, $\text{Chi}^2 = 18.1$) also when DBH is included as a covariate to control for genetic controlled variation in growth ($P = 0.0006$, $df = 1$, $\text{Chi}^2 = 11.9$) (Table 1). However, the Tukey analysis was not able to detect any significantly differences in C:N ratio between the specific full-sib families in both of the analyses.

Table 1. Test statistics from GLM analyses (P -values, Chi^2 , and df) of effects from full-sib family and DBH on the C:N ratio.

Effect Tests			
Source	DF	Chi²	P
Family	8	18.095	0.0205
DBH (cm)	1	11.908	0.0006

4: Growth rate of different full-sib families effect the C:N ratio of needles.

The C:N ratio in needles did not differ significantly between the full-sib families. ($P = 0.2283$) (Fig 4). Similar result was found for mean needle concentration of N ($P = 0.2329$).

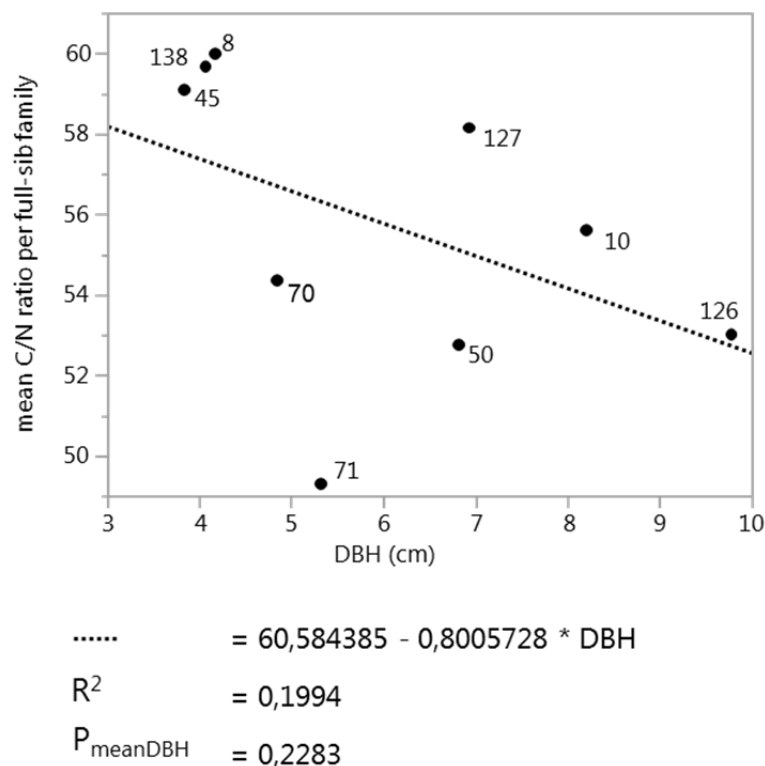


Figure (4). Linear regression of mean C:N ratio per full-sib family and corresponding mean DBH (cm). Line equation, R^2 , and P in legend.

The identification of the aphids resulted in 21 identified individuals in four species of the genus of *Cinara*. Most common, comprising 66 % of the community was *C. pruinosa* (14) followed by *C. piceae* (3), *C. piceicola* (3), and *C. pilicornis* (1). Three individuals of *Schizolachnus* spp. was found, these are however an aphid on Scots pine (*Pinus sylvestris*) and were considered as “tourists” (Roger Petterson personal communication Nov. 2015.) and disregarded in the statistical tests (fig 5).

5: The abundance of aphids is influenced by full-sib family and the C:N ratio of needles.

The abundance of aphids differed significantly between the full-sib families ($P = 0.0132$, $df = 8$, $\chi^2 = 19.3$) but not from the C:N ratio in needles ($P = 0.2266$, $df = 1$, $\chi^2 = 1.5$). However, follow-up analysis using Kruskal-Wallis method failed to detect any significant difference of aphid abundance between the nine full-sib families.

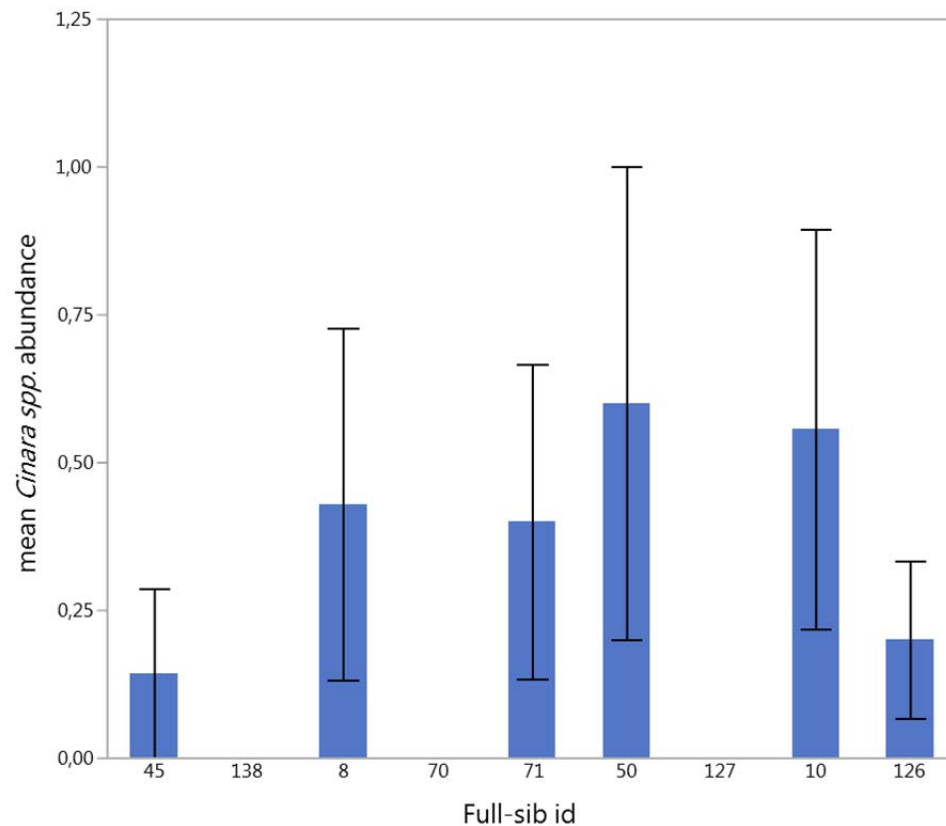


Figure (6.) Mean abundance of *Cinara* spp. on 9 different full-sib families of Norway spruce. Error bars show SE.

6: Growth rate of different full-sib families effect the abundance of aphids.

Growth rate in the different full-sib families did not have a significantly effect on mean aphid abundance ($P = 0.4700$, $R^2 = 0.0769$). In (fig 7) linear regression of mean per full-sib family *Cinara spp.* and DBH is shown with linear equation, R^2 -value, and p-value.

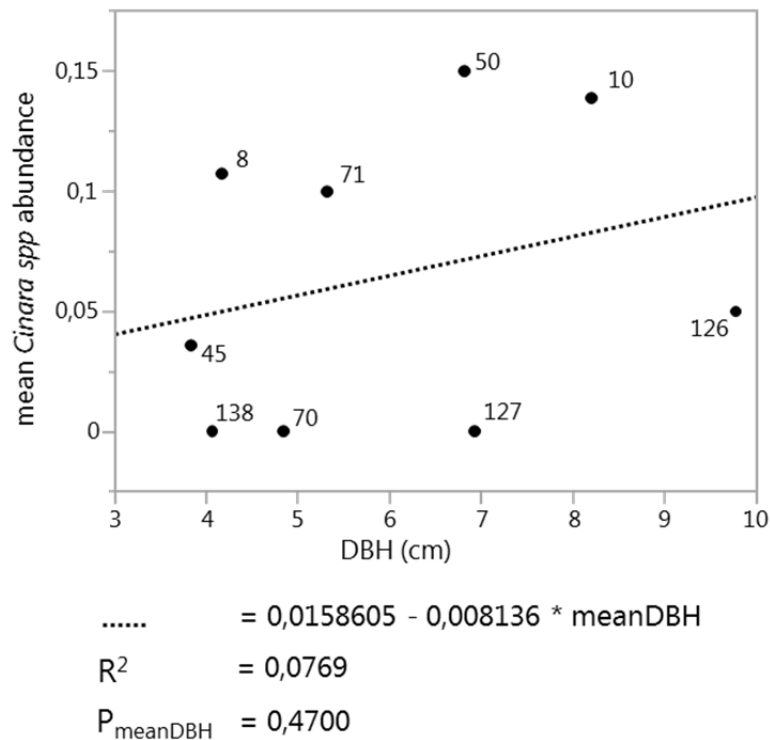


Figure (7) Linear regression of mean aphid abundance per full-sib family and corresponding mean DBH (cm) per full-sib family. Legend shows equation on the linear regression, p-value and R^2 .

Discussion

A general assumption in the field of community genetics is that genetically controlled variation in ecologically important plant traits will affect associated organisms and thus help in the formation of community phenotypes (Whitham *et al.* 2003). In this study, I was interested in exploring how genetically controlled variation in plant growth in Norway spruce may influence the nutritional status of the needles and further affect the abundance of aphids utilizing the tree. In line with the growth rate hypothesis it is clear from my results that the nutritional status (C:N ratio) of spruce needles correlated negatively with plant growth. However, although full-sib families also differed in both growth and C:N ratio, fast growing families did not necessarily have lower C:N ratios. The genetic origin of spruce trees also had a significant effect on the abundance of aphid. This effect could, however not, be explained by the nutritional status or growth rate of the host trees.

In line with my first hypothesis (H1) my results show that there is a clear difference in growth due to tree genetic origin. One full-sib family (126) differs significantly from five others (45, 138, 8, 70, and 71). The full-sib family 126 had a DBH twice as high compared with full-sib family 45, 138, 8, 70 and 71. The remaining tree full-sib families (50, 127, and 10) did not differ significantly from any of the other six or from each other. Such genetic controlled variation in plant growth as reported here is used in Swedish tree breeding programs to improve production potential of Swedish forestry. Today, seed orchards deliver 69 % of all spruce plant material planted in Swedish forests (Anon, 2014), and it is estimated that plants from such program have increased the production potential by about 20 % (Wennström *et al.*, 2008).

Given the general theory of growth rate and plant nutrition relationships (Elser *et al.*, 1996) it is relevant to explore how variation in growth such as shown in this study can play out to affect other ecologically important plant traits. In agreement with my second hypothesis (H2) I found a correlation between growth-rate of trees and the concentration of N (positive) and consequently the C:N ratio (negative) in the needles. This is consistent with Peng *et al.* (2011) that also found a positive relation between growth and N concentration in seven shrub species (*Bauhinia faberi*, *Periploca sepium*, *Hippophae rhamnoides*, *Sophora davidiana*, *Rosa roxburghii*, *Berberis wisoniae*, and *Pyracantha fortuneana*). Contradicting my fourth hypothesis (H4) the correlation fails to show when exploring this relationship on a family level, most likely due to the reduced power when pooling the data. However, the trend seems similar, despite the loss of statistical significance. Nevertheless, consistent with my third hypothesis (H3) full-sib family had a significant effect on the C:N ratio in needles. In this analysis the DBH was included as a covariate thus controlling for the effect of growth itself on C:N ratios. Taken together this suggests that the effect of full-sib family on C:N ratio is not a simple relation with among family differences in growth. Instead, part of the variation is explained by other genotypic differences which cannot be determined in this study.

In line with my fifth hypothesis (H5) full-sib family has an influence on aphid abundance. However, not as predicted through the C:N ratio. The mechanism of full-sib family effect on aphid abundance could consequently not be revealed in my study. Also, contrary my last hypothesis (H6) I found no correlation between growth-rate of the different full-sib families and aphid abundance. Despite the findings of a genetic effect on aphid abundance in this study the

mechanism of flow on effects of growth rate and C:N ratio seemed not to be valid. The reason for this may come from effects of other plant traits that may differ between genotypes. For example, Wimp *et al.* (2005) found that plant chemistry (e.g. secondary metabolites) can be an important factor that affects arthropod communities and also concluded that other genetic-based factors are likely involved. Although I cannot identify the specific mechanism, my results clearly show how plant genotype can affect plant chemistry as well as associated organisms. As stated above, Swedish tree breeding programme have a large impact on the growth of newly planted forests (Anon, 2014; Wennström *et al.*, 2008), such selection of specific genotypes could affect not only growth of spruce trees but also other ecologically important plant traits and in extension dependent organisms.

In working with my chemical analysis I assumed that trees with high concentrations of N in their needles and a low C:N ratio would imply that those needles would have a high nutritional value and be highly attractive for the aphids. However, the result contradicted that the C:N ratio influenced aphid abundance. Clearly, the genetic controlled differences in abundance of aphids could not be related to the genetically controlled levels of N in needles or growth rates of trees. The mechanism connecting the genetic control of aphid abundance remains to be determined in Norway spruce. More detailed studies on defensive substances could potentially help in this agenda. In fact, defensive chemicals come in a very large variety and concentration of C is a very rough measure of defensive capacity. For example, it is known that secondary metabolites can be used by insects in their own defence (Peterson *et al.*, 1987; Eisner *et al.*, 1974) and by feeding on them (Bernays & Woodhead, 1982; Kato, 1978). There is a great variation in effectiveness of defensive secondary metabolites on different species (Mattson, 1980), giving a great difficulty of using these to explain feeding behaviour of herbivores and nutrient content of foliage (Bennett & Wallsgrove, 1994).

There were no aphids found on the trees from three of the full-sib families. This is almost certainly a result of sampling intensity and should not be interpreted that these families are not utilized by aphids. Also, the within-family variation on aphid abundance was quite large which will affect the possibility to detect differences. This variation could have been reduced if sampling had been done when the aphids had been more active, i.e. earlier in the season. A more intensive sampling resulting in a greater dataset without full-sib empty of aphids had of course been preferred. Since the aphids in this study were collected late in the season, another interesting finding of Wimp *et al.*, (2005) is that toxic chemicals declined during the season which might increase the numbers of generalists. Genetically determined traits other than plant growth and needle nutritional status were not included in this study.

To conclude; in this study, I show that the genetic origin of Norway spruce have significant effects on ecologically important plant trait such as tree growth, N and C:N ratio in needles, and further can influence the abundance of aphids in tree canopies. However, growth rates of different full-sib families did not correlate with C:N ratios in needles or aphid abundance in tree canopies. Instead, it seems like there are strong among family patterns in the C:N ratio–growth rate relationship that does not correspond with the general trend of the population. Given these results, it seems possible that selection of plant material of certain genetic origin such as currently conducted in Sweden can influence how plant traits are expressed in the populations. If

these traits are of ecological significance we would also expect them to influence ecological processes.

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